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SEXUAL BEHAVIOR OF EUMENID WASPS (HYMENOPTERA: EUMENIDAE)

DAVID P. COWAN

Department of Biology, Western Michigan University, Kalamazoo, Michigan 49008.

Abstract.—The sexual behavior of five eumenid wasp species is described. This behavior differs sharply between species, and there is considerable within-species variation. Pairs of *Ancistrocerus antilope* remained together for 0.5–4 h and copulated one to four times. Pairs of *A. adiabatus, A. catskill,* and *Euodynerus foraminatus* came together, copulated once, and separated within 1–2 min. Pairs of *Parancistrocerus pensylvanicus* joined, and copulated once within about one min; but remained together for about 12 min and engaged in an elaborate postcopulatory behavior before separating.

The purpose of this article is to describe the sexual behavior of five eumenid wasp species and begin understanding these behaviors in an evolutionary context. It is now apparent that sexual behavior is best understood in terms of the two major aspects of sexual selection: 1) competition between males and its continuation as competition between their ejaculates (sperm competition) within a female's reproductive tract, and 2) female choice of males (Thornhill and Alcock, 1983). Among the eumenids, sexual selection has resulted in diversity with regard to behavior and structures used by males during courtship, the duration of single copulations, repeated copulations by a single pair of wasps, and post-insemination displays.

Newly emerged males of *Paraleptomenes miniatus* (Saussure) remain on their natal nest and mate with a sister (Jayakar, 1966; Jayakar and Spurway, 1966). In this species the sexes remain paired for nearly 2 h, and copulations which last only a few seconds are repeated every 15 to 20 min. Some other eumenids also have siblings mating at their natal nests: *Euodynerus foraminatus* (Saussure) (Cowan, 1979), *Ancistrocerus adiabatus* (Saussure) (Cowan, 1981) and probably *Epsilon* sp. (Smith and Alcock, 1980). In these species, a pair copulates only once for no more than a few minutes.

Species of *Paralastor* and *Abispa* have males that search for mates at wet areas where the females obtain building materials for nests (Smith and Alcock, 1980). Pairs of *Abispa ephippium* (Fabricius) fly together up into vegetation where they usually copulate twice, and following the last copulation the male performs agitated biting and pulling movements on top of the female before they separate. Mated pairs of *Paralastor* sp. copulate once for periods of 2–12 min, and the female may resist the male throughout or accept him quietly.

Some eumenids copulate for extended periods. Rau (1935) observed *Monobia*

quadridens (Linnaeus) mating for periods up to 30 min, and Cooper (1955) reports *Ancistrocerus antilope* (Panzer) copulating for periods of 12 to 28 min. In the course of various studies, I have had opportunity to make notes on the mating behavior of five eumenid wasps: *Ancistrocerus antilope, A. catskill* (Saussure), *A. adiabatus, Parancistrocerus pensylvanicus* (Saussure), and *Euodynerus foraminatus*. My observations not only reveal additional interspecific variation in mating behavior among the Eumenidae but also indicate significant intraspecific variation.

Methods

Wasps were obtained using trap-nests (Krombein, 1967) placed in rural areas of Kalamazoo, Emmet, and Cheboygan Counties, Michigan. The nests were open and the wasps were reared to adulthood in individual chambers. After eclosing as adults, they were segregated by sex and kept for several days in holding cages until used for mating experiments. While in the holding cages the wasps fed on sugar water.

I observed mating by placing one male and one female into cages approximately 30 × 30 × 30 cm. The cages had the top and one side made of glass and three sides of netting. Notes were recorded with a tape recorder. Pairs were left together in the cage until it was apparent that a male would no longer approach a female, a female successfully rejected a male, or they copulated and separated. These are behaviors that would have resulted in freely flying wasps becoming widely separated. Some *A. adiabatus* and *E. foraminatus* were not removed from their natal nests for rearing. Instead, they were reared and marked within their nests (Cowan, 1979, 1981). The nests were then placed outdoors, and the activity of freely flying wasps was observed. I use "courtship" to refer to the activities between a male's mounting and intromitting a female. "Active courtship" refers to periods during courtship when males were engaged in active behaviors that seemed to function in stimulating females. "Inactive courtship" refers to periods during courtship when males simply rode quietly on females. "Copulation" refers to the period of intromission when the genitalia were linked.

Results

Typically, when a male and female were placed together into a cage, the flying male oriented toward the resting or flying female and pounced on her dorsum. When mounted, the male was dorsal on the female facing the same direction. Unreceptive females of *A. catskill, A. adiabatus,* and *E. foraminatus* exhibited a distinct rejection behavior consisting of vigorous side-to-side rotation of her thorax around her longitudinal axis while curling her abdomen forward ventrally. This caused courting males to depart quickly. Receptive females tended to extend and lift the tips of their abdomens prior to linking genitalia. For most other aspects of mating, the species showed differences.

Ancistrocerus antilope (Panzer)

From a total of 75 pairings of *A. antilope,* 15 produced no mating behavior because the male did not approach the female. In 29 trials, the male oriented toward a female, mounted her, and either broke off contact immediately (n = 11) or courted and attempted copulation but eventually dismounted without mating

Table 1. Number of copulations per pair and mating duration (min) in *Ancistrocerus antilope*. n = sample size; $\bar{x}$ = mean; s = standard deviation.

Number of Copulations per Pair	n	Mean Duration of Pairing	Duration of Individual Copulations						
			First		Second		Third		Fourth
			$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$
1	7	29	23	13	—	—	—	—	—
2	20	88	30	6	30	9	—	—	—
3	2	145	27	15	28	6	26	6	—
4	1	245	27	—	40	—	44	—	34

(n = 18). In the 18 cases when males attempted but failed to copulate, 13 pairs were together for less than 5 min (mean, 1.3 ± 1.2 min), but on five occasions, the wasps remained together for 17, 20, 375, 240, and 237 min before separating. Females of *A. antilope* did not exhibit the vigorous rejection behavior observed with some other species. Sometimes they did shake from side to side during courtship, but this did not generally cause males to leave, and often the pair went on to copulate.

Thirty-one pairings resulted in copulations. Table 1 shows the number of copulations per pair, the total time wasps were paired, and the length of individual copulations for 30 matings. A mounted male maintained his hold on a female with his forelegs around the sides of her pronotum, his middle legs held out to the side, and his hind legs encircling her petiole. Using his antennae, he rapidly tapped and/or stroked the female's antennae (so rapidly that I could not determine the rate), but unlike some other species the antennal play did not seem to have any regular motion or periodicity. Sometimes, as a male fluttered his antennae, they appeared not to touch the female. In response, females held their antennae straight up.

While antennating a female, a male drew his abdomen forward so that its tip touched the side of her basal abdominal segments, he extruded his genitalia, and then stroked them down the side and underneath the female's abdomen. When his genitalia reached the tip of her abdomen, he tried to insert them into her genital chamber. The aedeagus and brushlike digitus (Snodgrass, 1941) of his genitalia were the structures that touched the females. The parameral spines were extended and kept clear of the female. Males repeated this probing behavior every few seconds, first from one side of the female's abdomen and then from the other, until achieving intromission. Males that did not successfully initiate copulation within 30–60 s broke off active courtship and simply rode on the female while she crawled or flew about. The males then resumed courtship after a varying period. If a male successfully linked genitalia, he remained dorsally on his mate but his abdomen's tip twisted about 90 degrees to the side to join with the female which also twisted her abdomen laterally about 90 degrees, thus bringing their abdomens venter to venter. During copulation, males embraced females with their middle legs in addition to the other pairs. This may have prevented females from flying. I never saw copulating pairs fly.

Some copulations proceeded with both male and female practically motionless. At these times, females stood with their antennae down, somewhat out to the

side, and males held their antennae in front of the female's face and waved or twitched them slightly. Quiet copulations contrasted with times when the wasps, particularly females, seemed agitated. Females kicked with their hindlegs at the tips of males' abdomens; and with their forelegs at the anterior ends of the males, particularly where they grasped females' prothoraces with their front legs. The females often walked about and wriggled their abdomens from side to side. These actions by females seemed to be attempts to dislodge males, and sometimes they seemed to cause the males to buzz their wings—perhaps in order to retain their hold on the females. Wasps exhibited all states between calm and agitated copulation.

The struggling during copulation did not follow a discernible pattern, but 15 pairs performed a stereotyped periodically repeated set of behaviors that lasted for 1–3 min midway through their last copulation. I saw it performed by three pairs that copulated once, 11 pairs that copulated twice, and by one pair that copulated three times. At these times, females appeared agitated as described above. Males started to tap at the females' raised antennae, and females gradually lowered their antennae. Then, simultaneously, the female wriggled her abdomen, both wasps raised their antennae straight up, and the male buzzed his wings momentarily. As a female wriggled, she rotated her abdomen so that the tip was no longer turned to the side, but was curled ventrally and drawn directly underneath the rest of the abdomen. Thus, her abdomen was not turned to the side and the male twisted his body even further around underneath his mate. As the wasps assumed this posture, their bodies seemed to stiffen and they remained motionless for a few seconds. The males lowered their antennae, waved them in front of the females, the females lowered their antennae, started to move about a little, relaxed their abdomens allowing them to rotate to the side, and the sequence was repeated at about 10 s intervals.

Copulation ended without an apparent struggle, and the unlinking of genitalia was not accompanied by separation of the pair. Once unlinked, several things might happen. Some males rode for a few seconds or minutes before flying away. Other times, after a period of inactivity, males initiated courtship behaviors identical to those before the first copulation and they either recopulated or the males flew away. The interval between successive copulations was 24 ± 25 min.

In the field, I have not seen *A. antilope* males frequenting nest sites where they might mate with emerging virgin females or with nesting females. Males were, however, common around flowers, and their behavior indicated they were searching for mates rather than feeding (Cowan and Waldbauer, 1984). They flew from flower to flower where they hovered or circled without landing. I once observed on a goldenrod inflorescence a female that was mounted by one male when a second male landed on top of them. The trio tumbled to the ground, the second male was displaced, and the female with the first male still mounted flew about 10 m up out of sight into nearby trees. It seems likely that males locate females at flowers, but once pairs have formed, they fly to less conspicuous sites for their extended copulations.

Ancistrocerus catskill (Saussure)

I observed 12 matings by *A. catskill* and timed the events in 11 of the copulations. Courtship was brief (9.5 ± 8.6 s) in 10 of the matings, but in one instance the male rode the female for 9.5 min before they linked genitalia. In eight pairings,

both sexes held their antennae erect and motionless, but in the other three the males tapped or stroked the female's antennae irregularly. Males simply probed with their genitalia at the tips of the females' abdomens; there was no repeated periodic abdominal stroking as seen in *A. antilope* or periodic probing as seen in *P. pensylvanicus* (see below).

As soon as a pair linked, a male released his leghold on a female's thorax and fell back behind her, attached only by his genitalia. A calm period followed (8 ± 6.5 s) while the female stood quietly and the male was immobile. This ended when females started wriggling and kicking at the tips of their abdomen, sometimes resulting in males being flailed about and banged against the substrate. Throughout this struggling by females, which lasted 72 ± 38 s, males remained impassive. In three copulations, the females brought their abdomens forward under their bodies and bit at the tips of the males' abdomens. Apart from the exceptional pairing with the long courtship, males and females of *A. catskill* were together for only 91 ± 33 s (n = 10) and their genitalia were linked for only 80 ± 38 s (n = 11). On four occasions, males remounted, but the females rejected them as described above.

Ancistrocerus adiabatus (Saussure)

I observed 12 matings by this small eumenid. Half the matings involved caged pairs, and the other half involved freely flying wasps near trap-nests where young adults were emerging. The events in all matings were similar, and I timed the events in six pairings. Mating by *A. adiabatus* is much like that of *A. catskill,* the primary difference being that *A. adiabatus* copulates more quickly.

As soon as a male mounted, he probed from the side at the tip of a female's abdomen with his genitalia and tapped or waved his antennae irregularly in her face. They quickly linked genitalia (within 12.4 ± 8.2 s); males immediately released their leg-hold, and fell back behind their mates. In two matings, the males waited 8 and 10 seconds after linking before falling back, and during this period both wasps were quiet with their antennae held erect. As with *A. catskill,* males dangling by their genitalia were motionless. Within 15 s after a male dropped back, females started kicking at the tips of their genitalia and wriggling their abdomens so that males were thrashed about. All the copulations ended when the females drew their abdomens forward and bit at the males. The wasps were paired for 41 ± 8.5 s, and they copulated for 31 ± 12 s. Once inseminated, females always rejected males that attempted mating.

Males of *A. adiabatus* return to the area of their natal nest as do males of *E. foraminatus* (Cowan, 1981), but *A. adiabatus* males did not regularly visit or defend nest entrances where virgin females were emerging. However, I did observe copulations by freely ranging wasps near nests that involved known siblings.

Unlike some other species of hole nesting eumenid wasps, males of *A. adiabatus* do not always develop more rapidly and emerge from the nest before their sisters. Occasionally, both sexes reached adulthood at the same time, the partitions between cells were broken down, and the adults had contact some time before exiting the nest. I suspect that sometimes siblings mate inside their nests before emerging.

Parancistrocerus pensylvanicus (Saussure)

My observations of mating by *P. pensylvanicus* are based on six females and one male from a single nest. The male courted all of the females but copulated

with only two. After the male mounted, pairs sometimes (n = 2) flew together, or the male immediately began courtship involving antennal play and a swiping probing motion at the tip of her abdomen with his partially extruded genitalia. The female stood with her antennae raised, and the male stroked them very rapidly two or three times (so rapidly that I was unable to be sure how many strokes were involved) and then paused momentarily with his antennae held erect before another series of rapid strokes. The bursts of antennal stroking came at about 1.5 s intervals. The abdominal probing differed from that of *A. antilope*. Rather than stroking the side of the female's abdomen, the male *P. pensylvanicus* only tapped or probed at the tip of a female's abdomen alternately from one side and then the other at 1.6 s intervals.

One pair did not copulate but remained together for 21 min. During this period, the male courted actively several times for about 1 min each. The remainder of the time, he simply rode on the female or the pair flew about the cage. When the male did court actively, he probed with his genitalia, and the female moved the tip of her abdomen to the side—away from the tip of his abdomen. In another trial, the male courted for about 1 min with similar results before dismounting. In the other two unsuccessful pairings, the male pounced on a female but quickly disengaged—once after the female wriggled her body, and the other time for no apparent reason.

In the two pairings that involved copulations, the male rode the female for about 10 s before starting antennal stroking and abdominal probing, and after about 35 s of active courtship they linked genitalia. After coupling, the male remained dorsal on the female with his abdomen positioned directly over the female's abdomen and curled ventrally to meet her genital chamber from the posterior ventral aspect. The male also continued to stroke the female's antennae in the same fashion used during courtship. He continued this behavior for 22 s in one case and 18 s in the other and then released his leg hold on the female so that he fell back attached only by the genitalia. The female immediately drew her abdomen forward ventrally and started biting and kicking at the tips of their abdomens. The struggling lasted for 15 and 8 s in the two copulations, and then their genitalia separated. As they unlinked, the male obtained a purchase on the female's abdomen with his legs and crawled back to the dorsal position.

After remounting, the male rode quietly on the females for 27 and 32 s before starting postcopulatory behavior. This behavior was very different from precopulatory courtship and did not seem to be an attempt by the male to remate. He raised his antennae, head, and abdomen and then brought them down seemingly forcefully on the female. The male repeated this behavior about five or six times a second for 2–3 s, paused for 5 to 20 s, and then performed another series. As the male bounced on the female, his mouth parts were between her head and thorax, his antennae tapped at about the middle of her flagellum, and his abdomen came down directly or slightly to the side of hers. Occasionally, the wasps flew together during postcopulatory activity. The male behaved this way for 12 and 13 min after the two copulations before dismounting.

Euodynerus foraminatus (Saussure)

I watched over 60 copulations by *E. foraminatus* and I timed the events in 26. Most of these observations involved freely flying wasps but seven pairs were

confined in cages. When mounted, a male grasped a female just under her tegulae with his forelegs; his middle legs were usually held out to the side but sometimes grasped the sides of a female's propodeum. His hind legs passed between her wings and clasped her basal abdominal segment.

Using the hooked apical segments of his antennae, a male simultaneously drew both of a female's antennae upward and stroked the length of her flagellum. This was repeated about once per second. At the same time, he probed with his abdominal tip around her abdominal venter and attempted to link genitalia. After mounting by a male, linkage occurred in 17 ± 38 s, and copulation proceeded quietly for 19 ± 10 s. During this quiet period, a male remained mounted, continued antennal stroking, and occasionally buzzed his wings. Females remained calm with their antennae held erect, or took a few steps. This quiet stage ended, and a struggle stage began, by movements of a female that started as side to side wriggling of the abdomen. These movements gradually became more vigorous, and a female used her hind legs to kick the male and to pry between their abdomens. Meanwhile, the male continued antennal stroking and flipped his wings occasionally, apparently to maintain balance. Struggling lasted 61 ± 31 s. When copulation terminated, males flew up from their mates.

The period between mounting and intromission is generally very short (about 5 s); however, for three copulations, all involving the same male, this period was 61, 97, and 170 s. I observed no other matings by this male. These copulations were the only three of the 60 I watched in which the male did not immediately begin antennal stroking and probing with his abdomen. This male simply mounted and rode passively on the females before starting active courtship, and then the copulations proceeded normally. The three females involved groomed or walked about during this precopulatory period, and one flew to a leaf about 50 cm away with the mounted male.

The struggle phase of one copulation did not end with the male flying up, but with the male releasing his hold with his legs and falling back suspended only by the genitalia. The female turned and bit the male on the tip of his abdomen, and the pair separated immediately. Falling back and hanging by the genitalia is typical when a copulating pair is disturbed by an intruding male (Fig. 1). The intruder lands on the copulating male which releases his grip and falls back. The intruder may then fly up, mount the female, stroke her antennae, and probe with his genitalia, while the original male remains firmly coupled to the female. If an intruder arrives before a male and female are securely linked, he may prevent copulation and cause the female to fly away unmated. Mated females always rejected males that attempted courtship.

Discussion

Mating behavior can be divided into three stages: 1) courtship; 2) copulatory behavior, including duration of copulation, number of copulations per pairing, position assumed by the sexes, and which sex is most active in terminating copulation; and 3) postcopulatory behavior. All stages of mating have probably been influenced by sexual selection acting thru male–male competition and female choice of males (Thornhill and Alcock, 1983). Once a male and female have come together, male–male competition may occur as males attempt to displace each other on the female, and it may continue as sperm competition, within a female's

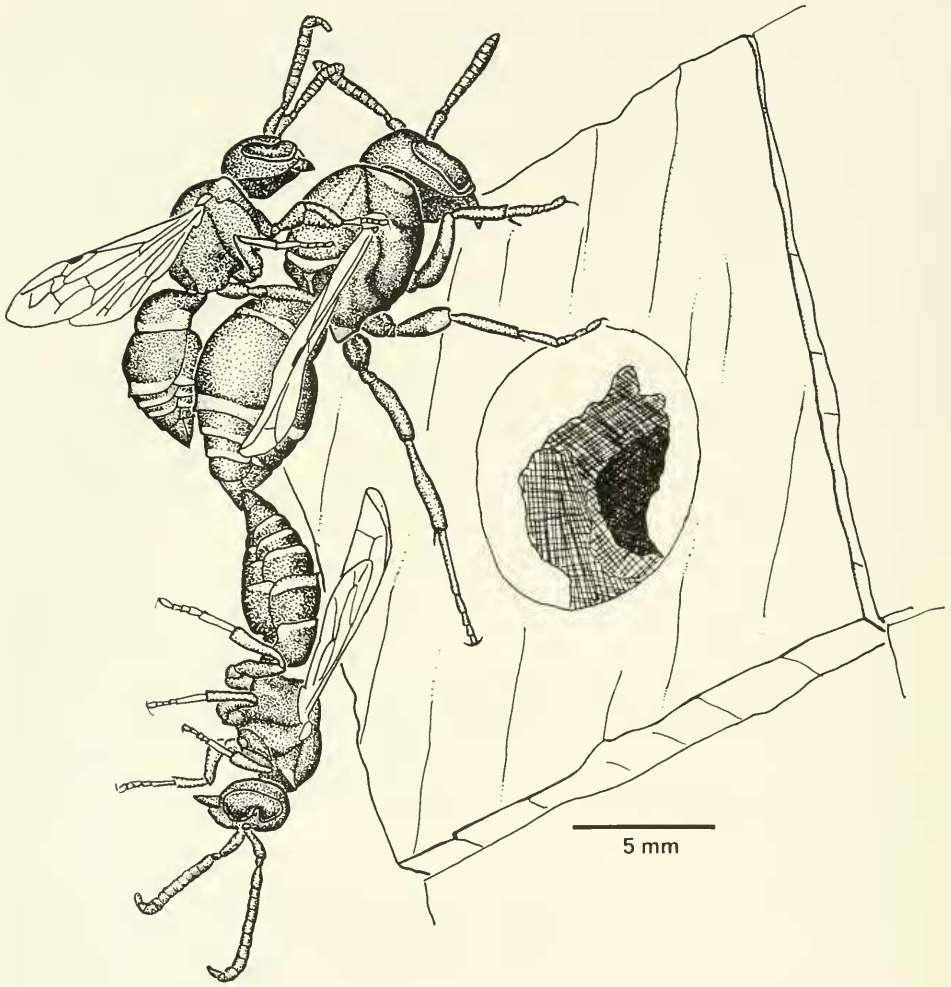

Fig. 1. A disturbed copulation of *Euodynerus foraminatus*. The wasp standing on the front of the trap-nest is a female. The two smaller individuals are males. The male hanging by his genitalia mounted the female and initiated copulation as she emerged from the nest. The male grasping the female is an intruder.

reproductive tract, between the ejaculates from different males. Females may exercise choice by simply making themselves available to favored males, by actively rejecting some males that court, or by remaining sexually receptive until having mated with a "choice" male. In the latter case, females may effectively "choose" the last male by allowing his sperm to fertilize her eggs.

Courtship.—Courtship communicates a variety of information, including species and sexual identity and information about the "quality" of potential mates. Consequently, some features of courtship may have evolved in the context of runaway sexual selection (Fisher, 1958). Eberhard (1985) argues that structures used by males to stimulate females during mating behavior will be most subject to runaway sexual selection, will evolve rapidly, and will thus be useful taxonomic characters. This seems to be the case for eumenid wasps. Antennal play by the male during

courtship is common, and the shape of the apical antennal segments on male eumenids is frequently used by taxonomists as a diagnostic character (Bohart, 1939a, b, 1940, 1948; MacLachlan, 1980). Males of *A. antilope* stroke females with their genitalia but males of *A. catskill* and *A. adiabatus* do not. Within the genus *Ancistrocerus,* male genitalia are rather uniform with the exception of *A. antilope* which has distinctive male genitalia (Bequaert, 1944). Males of *P. pensylvanicus* tap females with their genitalia during courtship, and for species in this genus male genitalia are distinctive (Bohart, 1952).

Duration of pairing.—Because pairs of some species of Eumenidae mate and separate within a minute, it seems unlikely that the longer matings exhibited by other species are necessary simply for sperm transfer. Thornhill and Alcock (1983) discuss several factors that could prolong copulating in insects. In addition to sperm, males may transfer nutrients to the female. If females mate with more than one male, then male-male competition may extend to competition between the ejaculates of the different males (sperm competition) within females' reproductive tracts. If males remove stored sperm from a female's reproductive tract or displace it with their own, extra time would be required. Or, a male might maintain contact with a female beyond the period needed for insemination to prevent other males from mating with her and displacing his sperm. Prolonged mating may induce non-receptivity of females.

The data needed to test these hypotheses for the wasps I watched are lacking. However, the species that mate quickly (*E. foraminatus, A. adiabatus,* and *A. catskill*) have monogamous females, and the species with the longest copulations (*A. antilope*) has females that do mate repeatedly with different males (Cowan and Waldbauer, 1984). This supports the hypothesis that extended copulation in these wasps has resulted from competition between males, sperm competition, or both.

Post-insemination displays and repeated copulations.—That males of *P. pensylvanicus* remain mounted on the female and engage in complex behaviors after completing insemination is surprising. Having transferred sperm, such activities would seem to be a waste of time, and one might expect the male to depart directly and resume other vital activities. Similar behaviors are known for a variety of Hymenoptera: *Abispa ephippium,* also in the Eumenidae (Smith and Alcock, 1980), a number of Chalcidoidea (Assem and Visser, 1976; Gordh and DeBach, 1978), and in the anthophorid bee *Centris pallida* (Alcock and Buchmann, 1985). Experiments with the pteromalid *Nasonia vitripennis* (Assem and Visser, 1976) and *C. pallida* (Alcock and Buchmann, 1985) show that post-insemination displays in these insects are important for inducing unreceptivity in the females. Normally, following a complete mating with post-insemination display, females of these two species reject the advances of additional males. However, when a male is prevented from performing his post-insemination display, females will mate again even though they had acquired sperm from the first male. Alcock and Buchmann (1985) speculate that the first male to mate with a female is sometimes genetically inferior. Should such a male be prevented from the post-insemination display and supplanted by a stronger male, then the female would obtain sperm from the genetically superior male. Thus, requiring post-insemination displays from males is viewed as an adaptation by females that increases their chances of obtaining a mate with "good genes."

Three species of eumenid are known to have multiple copulations for each pairing; *A. ephippium* (Smith and Alcock, 1980), *P. miniatus* (Jayakar, 1966), and *A. antilope*. Because the lifetime fecundity of females is low (probably not more than 25 eggs require fertilization (Cowan, 1981)), and because other closely related species mate only once, it seems unlikely that repeated copulations are needed to supply a female with adequate sperm. In fact, the stereotyped antennal movements and tensing of bodies observed during the last copulations by pairs of *A. antilope* suggest that physiological activities during the separate copulations may be different. Possibly, the repeated copulations are a means for males to access female receptivity: males attempt and engage in repeated matings until the female becomes unreceptive, thus decreasing the likelihood that the female will soon mate with another male. Repeated copulations by *A. antilope* may be comparable to the post-insemination displays of other Hymenoptera. Females may be less likely to remate quickly if a male demonstrates his "staying power" and thus "good genes" by remaining mounted and copulating repeatedly.

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